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THE SARCOSTYLES OF THE PLUMULARIDÆ.[1]

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THERE is no little confusion regarding the nomenclature involved in morphological discussions concerning the Hydroida, and nowhere is this fact more evident than in connection with certain interesting structures found in the Plumularidæ and variously called nematophores, protoplasmic processes, defensive zooids, sarcodal processes, Machopolyps, "Wehrthiere," and Nesselpolypen by the numerous writers who have investigated them. The first mention that I have been able to find of these structures is by Busk in Hunterian Lectures (MSS.), London, 1857, who called them "Nematophores," — a name subsequently used by various writers. Hincks afterward applied the name "sarcotheca" to the chitinous receptacle, and "sarcostyle" to the sarcodal contents, or rather defensive persons, inclosed within it. Without further discussion on this point, I will state that I use the word nematophore for the receptacle without necessary reference to its contents, and sarcostyle for the organ or person within, and it is to the latter that I invite attention at present.

[1] Read before section F at the Detroit meeting of the American Association for the Advancement of Science.

The hydroids have been carefully studied by so few zoologists that it may not be amiss to define the sarcostyle more explicitly before discussing it. A careful investigation of any plumularian hydroid will disclose the fact that beside the hydrothecæ containing the hydroid polyps or hydranths, there are numerous usually minute chitinous cups containing an exceedingly interesting structure, which in life is characterized by amazing extensibility. Allman in 1864 described it as "a soft granular mass which could send forth very extensible processes capable of being greatly protruded, and then so completely retracted as to apparently disappear. These processes have the power of sending forth pseudopodia, as does the amœba, and act in many respects as do certain rhizopods." This author considered that these processes were composed of protoplasm, pure and simple.

When, however, the more refined and modern histological technique was applied by Hamann to the investigation of the sarcostyles, it was discovered that they were much more complicated structures than was at first supposed; that they were made up of several histological elements; namely, an ectodermal layer surrounding an axial portion composed of endodermal cells, the ectoderm and endoderm being separated by a structureless membrane or "Stutzlamelle." The distal part of the sarcostyle contains nematocysts or nettling cells. This author (Hamann)[1] concluded that the enormous extensibility of the sarcostyle was due to muscle fibrillæ, and regards the entire sarcostyle as a degraded person or hydroid polyp in which the mouth and body cavity have been obliterated.

In the same year, 1882, C. de Merejkowsky[2] announced that the histological elements were ectoderm and endoderm with a dividing membrane, and that the motile part was composed of ectoderm alone, the ectodermal cells being *immersed in a contractile structureless protoplasm.* To this latter substance he attributed the enormous extensibility of the sarcostyle and the pseudopodia-like processes originally described by

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[1] Der Organismus der Hydroidpolypen. *Jenaische Zeitsch. f. Naturw.*, Bd. xv, pp. 17, 18, 65.

[2] *Arch. de Zool. Exp. et Gen.*, vol. x, pp. 583–610.

Allman. This author regards the sarcostyles as degenerate individuals of the hydroid stock, serving the purpose of defensive organs and possibly also as aid in the nourishment of the colony.

Weismann, in his *Die Enstehung der Sexualzellen bei den Hydromedusen*, denies the presence of the interstitial protoplasm in the ectodermal portion and contends that the pseudopodia are from the ectoderm cells themselves.

In the same year, 1883, von Lendenfeld[1] made a very elaborate study of the sarcostyles. In addition to the ectoderm, endoderm, and "Stutzlamelle" already mentioned, he found a differentiated ectodermal muscle layer, in which are large ganglion cells in Plumularia. In certain species of Aglaophenia and Plumularia he found sarcostyles furnished with adhesive cells similar to those found in ctenophores, but differing from them in not having a spirally rolled thread.

Dr. Carl F. Jickeli[2] agrees with most of the other writers concerning the histology of these structures, but has a unique idea of their homology. He thinks that the sarcostyles are homologous with the capitate tentacles of many species of hydroid polyps. I believe that he has no supporters in this view.

No other investigations of sufficient importance to discuss in this connection have been made so far as I know, with the exception of my own work in 1895 at Plymouth, England,[3] and at Naples, where I made careful studies of these structures in the living plumularians and by means of serial sections.

The histology of the sarcostyles, as held by most of the above writers, shows an outer layer of ectoderm and an inner layer of endoderm, these two layers being separated by an apparently structureless membrane called by the German writers the "Stutzlamelle." The endodermal layer appears to be a solid core in stained and sectioned preparations, and is so described by most writers. Under favorable conditions living specimens may be examined under a high power, and by a proper management of light the cell boundaries, muscle, and indeed almost every histological detail may be distinctly seen and the movements followed. It was while making such examinations of living sarcostyles at Naples in 1895 that I found an unexpected proof that the axis of the sarcostyle is not a solid rod, but a delicate collapsible tube, the cavity of which is strictly homologous with the body cavity of the hydranth. While studying a living sarcostyle under a $\frac{1}{12}$ oil-immersion lens, the endodermal axis, as it is called, was very sharply defined, being separated from the ectodermal layer by the "Stutzlamelle." Much to my surprise, I saw an amœboid cell pass quickly along the exact center of the axis. The cell was largely composed of highly refractive granules and exhibited very active amœboid movements, sending forth well-marked pseudopodia and constantly changing form. This mysterious cell appeared to be engaged in traveling back and forth between the distal and proximal end of the axial cavity of the sarcostyle. Its progress was unimpeded and completely demonstrated to my mind the presence of an axial cavity in the sarcostyle. After having once seen this cell, I looked for them in other sarcostyles and found them in nearly every one examined. The species under observation was *Aglaophenia helleri.* I afterward found similar cells in the endoderm of various parts of the plumularian colony, particularly in the stem. In such localities, however, they did not move from place to place, but nevertheless sent forth numerous pseudopodia and exhibited amœboid change of form.

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[1] Ueber Wehrpolypen und Nesselzellen. *Zeit. f. wiss. Zool.*, Bd. xxxviii, pp. 355–371.

[2] *Morphol. Jahrb.*, Bd. viii, pp. 580–680.

[3] See C. C. Nutting, Notes on Plymouth Hydroids. *Journ. Marine Biol. Assoc.*, February, 1896, p. 153.

This demonstration of an axial cavity in the sarcostyle is of considerable interest, in view of the fact that it furnishes the last and much-desired link in the evidence needed to demonstrate the homology of the sarcostyle. It can no longer be doubted, it seems to me, that the sarcostyle is the homologue of the hydranth; that it is, in fact, a true "person" of the hydroid colony, being composed of ectoderm, "Stutzlamelle," endoderm, and body cavity. It lacks only tentacles to make it a hydranth, but we know that certain hydroids, *e.g.*, Protohydra, have undoubted hydranths without tentacles.

Curiously enough, one of the earliest observers of nematophores published in 1863 a figure of a sarcostyle which was represented as having a body cavity. The author referred to is Semper, and the figure is found in the *Zeitschrift für wiss. Zoologie*, Bd. xiii, Pl. XXXVIII, Fig. 4 *a*.

The conclusion that sarcostyles are morphological persons of the colony is borne out by almost every known fact concerning them. Embryological investigation shows that they are formed in almost exactly the same manner as the hydranths, and that they make their appearance as early as the latter and often earlier. It is possible, moreover, to point out a series of forms leading from the so-called "fighting zooids" of Hydractinia to the typical nematophores of the Plumularidæ. In the genus Ophiodes we find organs or persons almost exactly intermediate between the Hydractinia and true sarcostyles. Prof. Baldwin Spencer has lately described a new family of Hydroida, called the Hydroceratenidæ, evidently closely allied to the Plumularidæ, with numerous fighting persons which are histologically almost identical with true nematophores; the extreme extensibility, however, of the latter has not as yet been observed in the former.

There appears also to be a curious cross relation between the dactylozooids of the Millipora and the sarcostyles, if such they be, of the Hydroceratenidæ.

Among the many perplexing questions in this connection is the one raised by Professor Allman, who very strongly urges the relationship between the nematophores and the denticles of the graptolites. His argument would lead to a belief that the ancestors of the Plumularidæ may be the graptolites; that the nematophores of the former are the homologues of the denticles of the latter; that we have in the sarcostyle the original type of the hydranth; and that the present hydranth is really a very highly specialized sarcostyle.

As before indicated, the sarcostyles often precede the hydranths in the development of the colony, and would thus appear to be an older structure in phylogeny.

I was unable to confirm Merejkowsky's statement that the extensible part of the sarcostyle was composed of ectodermal cells immersed in free protoplasm. Indeed, it appears that no other author has been able to demonstrate this certainly unique and surprising arrangement. Neither could I find the muscle bundles and ganglion cells of von Lendenfeld, although this purely negative evidence should not be allowed to have much weight. The adhesive cells were found in several species of Aglaophenia, and observed in action; the observations confirm very decidedly the description given by their original describer, von Lendenfeld.

There has been considerable discussion concerning the probable use of the sarcostyles. My own observations on the living organisms would indicate that they serve several distinct functions.

1st. *Defense.* In many cases, especially in the genera Aglaophenia, Lytocarpus, and Cladocarpus, the distal part of the sarcostyle contains a battery of very large and formidable nematocysts or stinging cells. The threads of these cells are projected all together when a large or dangerous enemy approaches too near the adjacent hydranth. It is probable that the cnidocils of these nematocysts must be touched before the battery is discharged. Some species of Lytocarpus have such effective batteries that their sting is severely felt through the human cuticle, a very unusual thing among the Hydroida. The nematocysts themselves do not leave the nematophores when their threads are projected.

2d. *Prehension of food.* This is effected by the adhesive cells, which are situated on the extensible part of the sarcostyles of many species. Von Lendenfeld gives an excellent description of the capture of small crustacean zoæa. From his account it appears that the prey is first paralyzed by the nematocysts in the tentacles of the hydranths, and then secured by the adhesive parts of the adjacent sarcostyles which stick firmly to the smooth chitinous covering of the crustacean. After this attachment is formed, the contraction of the sarcostyle brings the victim again within the reach of the tentacles, which convey it to the mouth of the hydranth.

3d. *The removal of refuse or decomposing organic matter.* This function of the sarcostyles has been suggested by several writers. I have on many occasions noted that the sarcostyles are very active after certain parts of the colony have been mutilated or where the hydranths are undergoing disintegration. While studying *Plumularia pinnata* at Plymouth I saw astonishing exhibitions of activity on the part of the sarcostyles in the vicinity of mutilated gonangia. Their extensibility was incredible and apparently without limit. They would climb over the top of the gonangia and scour the inside, they would wind round and round the stem and branches in a perfect maze of apparently protoplasmic threads, and yet be able to unsnarl themselves with the greatest ease and afterward disappear entirely. Dead hydranths seemed particularly attractive to them, and it appeared as if they actually devoured or in some way absorbed the organic matter of the disintegrating polyps, so that not a trace remained within the hydrothecæ in a very short time after the sarcostyles attacked them.

4th. *Holding together adjacent corbula leaves until their edges unite.* This is a novel use of the sarcostyle, discovered by myself while working out the embryology of the corbula, or fruit receptacle, of *Aglaophenia pluma* at Plymouth. The corbula is a pod-shaped structure made up of a number of ribs or leaves, which are separated first, but afterward coalesce to form the mature corbula. Along the edges of these leaves are rows of nematophores.

While examining a young corbula of a living colony, I noticed that the sarcostyles along the edges of the leaves were exceedingly active and that they were stretching across from one leaf to the next, to which they adhered by their adhesive ends. "It appeared as if these sarcostyles served as a temporary attachment to hold the edges of the two leaves together, while the edges themselves were connected by trabeculæ of cœnosarc which rapidly formed a stronger and permanent connection. The perisarc of the edges of the leaves seemed exceedingly thin and in places appeared to be wanting. A contact having been established between the adjacent leaves, the permanent attachment was soon formed and the cœlomic cavities of the leaves established connections at these points.

A little later currents of water bearing granules were seen to flow in active streams from one leaf to the other."[1]

In this case it appeared as if the sarcostyles served to hold the edges of the leaves together while the permanent connection was being established, after which the sarcostyles loosened their hold and retracted into their respective nematophores.

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[1] C. C. Nutting, Notes on Plymouth Hydroids. *Journ. Marine Biol. Assoc.*, February, 1896, p. 153.